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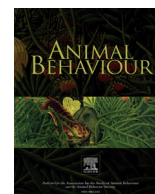
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Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific



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The annual 29 000 km long migration of the bar-tailed godwit, *Limosa lapponica baueri*, around the Pacific Ocean traverses what is arguably the most complex and seasonally structured atmospheric setting on Earth. Faced with marked variation in wind regimes and storm conditions across oceanic migration corridors, individuals must make critical decisions about when and where to fly during nonstop flights of a week's duration or longer. At a minimum, their decisions will affect wind profitability and thus reduce energetic costs of migration; in the extreme, poor decisions or unpredictable weather events will risk survival. We used satellite telemetry to track the annual migration of 24 bar-tailed godwits and analysed their flight performance relative to wind conditions during three major migration legs between nonbreeding grounds in New Zealand and breeding grounds in Alaska. Because flight altitudes of birds en route were unknown, we modelled flight efficiency at six geopotential heights across each migratory segment. Birds selected departure dates when atmospheric conditions conferred the greatest wind assistance both at departure and throughout their flights. This behaviour suggests that there exists a cognitive mechanism, heretofore unknown among migratory birds, that allows godwits to assess changes in weather conditions that are linked (i.e. teleconnected) across widely separated atmospheric regions. Godwits also showed adaptive flexibility in their response not only to cues related to seasonal changes in macrometeorology, such as spatial shifting of storm tracks and temporal periods of cyclogenesis, but also to cues associated with stochastic events, especially at departure sites. Godwits showed limits to their response behaviours, however, especially relative to rapidly developing stochastic events while en route. We found that flight efficiency depended significantly upon altitude and hypothesize that godwits exhibit further adaptive flexibility by varying flight altitude en route to optimize flight efficiency.

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Wind has received more attention and is more integral to optimal migration theory for winged organisms than any other aspect of movement ecology (Alerstam, 1979, 2011; Alerstam & Hedenström, 1998; Chapman et al., 2010; Felicísimo, Muñoz, & González-Solis, 2008; Gauthreaux, Michi, & Besler, 2005; Liechti, 2006; Liechti & Bruderer, 1998). Because air can move as fast as or faster than most winged organisms, strong selection pressure should favour strategies that undertake migration under advantageous

atmospheric conditions (Åkesson & Hedenström, 2000; Alerstam, 1979, 2011; Liechti, 2006; Mellone, López-López, Limiñana, & Urios, 2011; Shamoun-Baranes, Bouten, & van Loon, 2010; Shamoun-Baranes & van Gasteren, 2011; Shamoun-Baranes, Leyrer, et al., 2010; Williams & Williams, 1990). The foundation of wind selection and optimal migration theory is rooted in case histories of mostly landbird species that alternate bouts of migration with stopovers to refuel as they move long distances across the landscape (Rappole, 2013). Similar migration strategies are commonly used by waterbird species with aquatic stopovers (e.g. Felicísimo et al., 2008). Sometimes terrestrial migrants make incorrect assessments of synoptic-scale winds at departure or en route that create shortcomings in their travel energy budgets (Drent, 2006; citations in Newton, 2008; Richardson, 1977, 1990; Shamoun-Baranes & van

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Gasteren, 2011). To compensate, most landbirds and waterbirds stop more frequently or stay longer at a site until conditions improve (Ma et al., 2011; Schmaljohann, Fox, & Bairlein, 2012; Weber, Alerstam, & Hedenström, 1998). Endurance migrants (Hedenström, 2010), however, comprise a small but growing suite of avian species discovered to fly long distances nonstop across inhospitable areas where stopover sites are scarce or nonexistent. For individuals of these species, which often migrate through complex atmospheric structure, death is a likely outcome if fuel stores are insufficient or not managed in relation to atmospheric conditions (Kemp, Shamoun-Baranes, Dokter, van Loon, & Bouten, 2013; Kerlinger, 1989; Mellone et al., 2011; Piersma, 1998).

Recent applications of remote-tracking technology have revealed feats of avian migration in which individuals sustain nonstop flight for over a week (Battley et al., 2012; Gill et al., 2009; Johnson et al., 2012; Klaassen, Alerstam, Carlsson, Fox, & Lindström, 2011; Minton et al., 2010; Piersma, 2011a). For such flights birds face decisions not only about when to depart (Grönroos, Green, & Alerstam, 2012; Piersma, Zwarts, & Bruggemann, 1990; Yamaguchi, Arisawa, Shimada, & Higuchi, 2012), but also where to fly en route since winds may vary in direction and strength both horizontally and vertically (Ahrens, 2007; Dokter, Shamoun-Baranes, Kemp, Tijm, & Holleman, 2013; Mellone et al., 2011). Thus, after take-off, birds should position themselves optimally within the three-dimensional air space to manage fuel relative to distance, time, and possibly osmotic balance (for latter see: Gerson & Guglielmo, 2011; Klaassen, 2004). When and where to fly are also functions of the predictability and variability of atmospheric conditions along a migration corridor (Piersma & van de Sant, 1992).

If migration corridors span great expanses of latitude they invariably cross one or more of the Earth's well-defined zonal belts of wind and pressure. These zones are not trivial in extent (most encompass 20° of latitude). At the hemispheric scale, zones are associated with wind directions and speeds that are grossly predictable by location and season (Ahrens, 2007). However, there are also inherent elements of variability, ranging from short-term synoptic events such as cyclones (which vary in timing, strength and track), to long-term (interannual or decadal) cycles of coupled oceanic–atmospheric interactions (Chand & Walsh, 2011; Cooper, Whysall, & Bigg, 1989; Di Lorenzo et al., 2010; Eichler & Higgins, 2006; Smith, Moise, & Colman, 2012; Ulbrich, Leckebusch, & Pinto, 2009). Ability to accommodate such a broad range of migratory conditions should be reflected in the life-history strategies of long-lived, long-distance migratory species.

Studies of wind profitability in migrating birds flying nonstop have to date been limited to passage of migrants through only one, or at the juncture of two, of these zones, mostly the trade-wind zones, with fewer studies of birds in the zones of westerly winds (e.g. Kemp et al., 2013; Mellone et al., 2011; Shamoun-Baranes & van Gasteren, 2011; Stoddard, Marsden, & Williams, 1983; but see Felicísimo et al., 2008 for multizone transit by seabirds). In this study we assess wind profitability of a migratory shorebird species, the bar-tailed godwit, *Limosa lapponica*, whose annual migration entails three nonstop flights, each of about a week's duration or longer, representing a 29 000 km long circumnavigation of the central and western Pacific Ocean (Fig. 1; Battley et al., 2012; Gill, Piersma, Hufford, Servranckx, & Riegen, 2005; Gill et al., 2009). During these epic flights birds cross five of the six zones of global wind where they can be subjected to extreme spatiotemporal variability in atmospheric conditions (Mesquita, Atkinson, & Hodges, 2010; Overland, Adams, & Bond, 1999; Pickart et al., 2009; Terry, 2007).

In this study we evaluated the flight efficiency of satellite-tracked bar-tailed godwits in terms of the predictability and variability of wind assistance during departures and subsequent en

route phases of the three legs of their migration. We did this first in terms of a 'decision space' in which we evaluated the timing of departure with respect to environmental conditions (cues) available to godwits at the departure points. For the en route portion of the godwit's migration, we assessed their 'option space' by evaluating the along-track wind components of each flight corridor as established by the satellite-derived locations of tracked godwits. We questioned if there was one set of cues used throughout the annual migration or, given the stark contrast in atmospheric regimes that godwits must navigate each year, if cues were site, seasonal and altitude specific. We examined the working hypothesis that atmospheric structure over the Pacific Ocean does affect the timing and routes of bird migration. We predicted that the flight responses of bar-tailed godwits involved context-specific behavioural decisions related to seasonally structured and predictable elements of atmospheric circulation that occur over each leg of their annual migration.

METHODS

Atmospheric Setting

The structure of the winds across the Pacific is largely a function of alternating, latitudinally layered bands of high and low pressure (Fig. 1). These produce several prominent wind zones that are defined not only by winds of prevailing direction and strength, but also by their characteristic seasonal synoptic-scale disturbances (e.g. tropical, subtropical and temperate cyclones). The most prominent zones of winds in each hemisphere are the Polar Easterlies, Westerlies and Trade Winds, but most of the godwit's migration traverses the Westerlies and Trades (Fig. 1). The prevailing Westerlies blow west to east in broad bands north and south of the equator (between 30° and 60° N/S latitude). In the Northern Hemisphere these near-surface winds are predominantly from the southwest; in the Southern Hemisphere, from the northwest. In both hemispheres they are buffered by narrow bands of high pressure (subtropical high pressure cells) that occur between 20° and 35° N/S and are characterized by subsiding dry air and weak winds. The Westerlies, which are driven by these subtropical high pressure cells, in turn transition into the Northeast and Southeast Trade Winds, which blow steadily at about 5–6 m/s within 30-degree-broad bands of latitude that converge at the equator (Fig. 1). Within this area of low pressure convergence (Intertropical Convergence Zone; ITCZ), there is strong convection (rising air) and heavy rainfall. A portion of the ITCZ, the South Pacific Convergence Zone, occurs where the Southeast Trades meet with semi-permanent easterly flow from the eastern South Pacific belt of anticyclones (Fig. 1).

The godwits' atmospheric setting has additional layers of complexity because superimposed on this generalized flow are variable features of daily weather and multiyear oscillations in atmospheric structure and climate. Winds vary (1) diurnally as air masses heat and cool, (2) weekly to monthly as synoptic disturbances develop and move in waves across well-defined portions of the Pacific and (3) interannually in association with phases of large-scale atmosphere–ocean interactions such as the Western Pacific Monsoon, El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO). The position of a bird in this atmospheric setting will substantially increase or reduce its travel speed and thus energetic costs of migration.

Transmitter Deployment

We tracked flights of 24 godwits using satellite transmitters (PTTs) deployed on birds captured on their breeding and

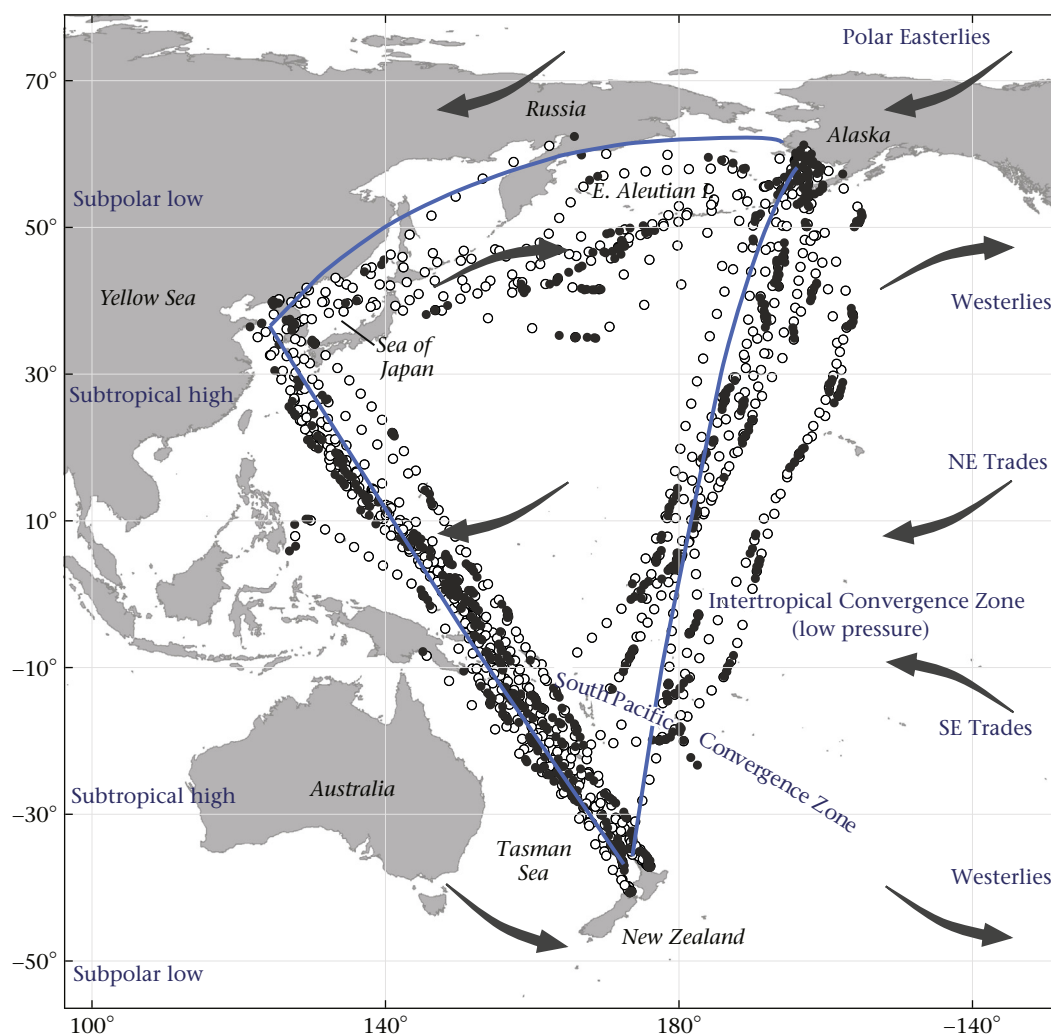


Figure 1. Migration tracks of bar-tailed godwits, *Limosa lapponica baueri*, obtained by satellite telemetry (black filled circles; $N = 678$) and interpolated to 6 h intervals (open circles) along intervening orthodromes. Data represent nonstop flights from the point of origin to the first landfall or the end of data reception along each leg of the annual migration: New Zealand to Yellow Sea, Yellow Sea to Alaska, Alaska to New Zealand and eastern Australia. Zones of global high and low pressure are shown on the left and wind zones are shown on the right. Arrows show broad-scale prevailing wind directions (after Ahrens, 2007). Thin blue lines depict great-circle routes on each migration leg. Map is a Plate Carrée projection.

nonbreeding grounds between 2006 and 2010. We used three models of PTTs: approximately 26 g and 19 g battery-powered models that were surgically implanted in the coelomic cavity (Mulcahy, Gartrell, Gill, Tibbitts, & Ruthrauff, 2011) and a 9.5 g solar-powered model that was attached to the lower back using a leg-loop harness (Gill et al., 2009). PTTs were deployed on 15 female godwits (26 g implant: $N = 14$ females; 19 g implant: $N = 1$ female) and nine male godwits (solar implant: $N = 8$ males; 26 g implant: $N = 1$ male). Birds were caught with bow traps, mist nets or cannon nets and banded under permits from the New Zealand Department of Conservation, Auckland University, Massey University and the U.S. Geological Survey's Alaska Science Center. Individuals were given uniquely coded leg flags to facilitate subsequent visual detections and are referenced accordingly in this paper. Surgical implantation was conducted on anaesthetized birds under sterile conditions by licensed veterinarians who have performed this technique during more than 3000 surgeries in more than 30 species of birds (Mulcahy, n.d.). Antennas were contoured to the bird's in-flight horizontal plane to reduce potential drag (Barron, Brawn, & Weatherhead, 2010; Bowlin et al., 2010; Pennycuick, Fast, Ballerstädt, & Rattenborg, 2012). Details of the surgical procedure, including preparation, anaesthesia, surgery,

vital signs monitoring, recovery, release, weights and dimensions of transmitters, and load ratios of the individual birds in this paper are treated in Gill et al. (2009) and Mulcahy et al. (2011) and were approved by Institutional Animal Care and Use Committee (IACUC) guidelines of the University of Auckland, New Zealand, and the U.S. Geological Survey, Alaska Science Center (IACUC 070504-4).

Data Acquisition and Preparation

Transmitters implanted in godwits captured in New Zealand in 2007–2008 ($N = 11$) were programmed to report with a duty cycle of 6 h on: 36 h off. Those implanted in godwits in Alaska in 2006 were programmed to report 8 h on: 24 h off ($N = 4$) and in 2010 for 6 h on: 36 h off ($N = 1$). The duty cycle for solar-powered transmitters (6 in New Zealand in 2007; 2 Alaska in 2006) was for 10 h on: 48 h off. The loss of a few birds en route, shedding of some external PTTs, and battery failure reduced sample sizes throughout the course of the annual cycle. Data processing and filtering (Douglas et al., 2012) followed procedures in Gill et al. (2009) and Battley et al. (2012). PTTs produced an average \pm SD of 5.3 ± 2.8 locations per duty cycle after filtering. Elapsed time between duty cycles spanned an average \pm SD of 1.4 ± 0.5 days.

Routes and distances between locations were assumed to follow great circles (orthodromes). The filtered satellite locations ($N = 751$; see Results) served as reference points for interpolating locations at 6 h intervals along the intervening great circle routes (Fig. 1). A 6 h periodicity (0000, 0600, 1200 and 1800 hours Coordinated Universal Time, UTC) was chosen to match the temporal resolution of the wind data (see below). The beginning and ending points of each migration leg for an individual were assumed to be the first and last terrestrial (or last open-ocean) locations recorded during each of its flights. Since tracking relocations were intermittent due to PTT duty cycles and satellite overpass schedules, we estimated departure times by extrapolating the net tracking velocity during the first en route duty cycle from the first en route location back to the departure location. During the initial 3000 km of the migration from Alaska to New Zealand, both average flight speed and deviation of tracks from a great-circle route varied by less than 10% (Gill et al., 2009). If we assume a 10% error range in both the rates and distances that were used to extrapolate the departure times on the three migration legs, then 50% of our estimates were within 8 h and 90% were within 16 h of the true departure times. Any uncertainties in the timing of departure, however, would not have been propagated over the migration because each subsequent en route satellite location provided an empirical tie-point between the tracking and wind data. Arrival times were analogously estimated using velocity data from the last en route duty cycle extrapolated from the last en route location forward to the arrival location.

Wind Analysis and Flight Performance

To analyse actual flight performance vis-à-vis winds, we linked each bird's satellite-derived ground speed with reanalysis-derived winds. Ground speed (distance travelled across the Earth divided by elapsed time) and direction of a bird in flight are a function of both the bird's speed and direction through the air (air component) and the wind speed and direction (wind component) (Grönroos et al., 2012; Shamoun-Baranes, van Loon, Liechti, & Bouten, 2007). Satellite-tracking data for each godwit yielded minimum estimates of the bird's ground speed because we prescribed direct flight paths between the observed locations. For consecutive interpolated locations we assumed constant ground speed. We used u-v vector wind speed data from the global ERA-Interim reanalysis (Dee et al., 2011; Simmons, Uppala, Dee, & Kobayashi, 2006) to decompose the tracking (ground) vectors into air and wind vector components. Wind speed and direction were calculated at each interpolated 6 h godwit location as an inverse-distance weighted average of the four surrounding wind speeds from the 1.5-degree resolution ERA-Interim grid (Appendix, Fig. A1). Winds at the start and end of each 6 h tracking vector were averaged to derive the associated wind component and then the wind component was subtracted from the tracking vector to derive the bird's air component. Because we were unable to determine the specific altitudes at which godwits flew (PTTs with pressure sensors were not available), we assessed the vertical structure of wind conditions by extracting and analysing wind and air vectors at six geopotential heights: 1000, 925, 850, 700, 600 and 500 hPa, which roughly correspond to 100, 800, 1500, 3000, 4000 and 5000 m above sea level, respectively. We limited our analysis at 500 hPa since few studies have reported birds routinely migrating higher than 5000 m above ground level (citations in Newton, 2008).

We follow Alerstam (1979) in presenting results as air-to-ground ratios (AGR), calculated as the bird's air speed divided by its ground speed. Magnitude of the ratio reflects the degree to which winds either assisted (<1) or impeded (>1) the flight trajectories. Units of the ratio can be interpreted as either speed or

distance. For example, a ratio of +2.0 (strong wind resistance) indicates that a bird's air speed was twice its ground speed, or equivalently, that wind conditions required the bird to fly through the air column twice as far as it progressed across the landscape. Conversely, a ratio of 0.5 (strong wind assistance) indicates that a bird's air speed was half its ground speed and that it covered twice the ground distance that it would have covered in still air.

We examined variability in AGR values over space, time and altitude to evaluate individual behavioural choices at the time of departure and en route during migration. For individual birds at each of the three departure sites (New Zealand, the Yellow Sea, Alaska), we calculated AGR values for the first 30 h of the flight ($AGR_{30\text{ h}}$; mean of the first four full 6 h tracking segments plus any initial segment <6 h) at each of six geopotential heights (1000, 925, 850, 700, 600 and 500 hPa). We calculated AGRs for the actual dates of departure and for each of the 7 days preceding and following that date. This 15-day set of $AGR_{30\text{ h}}$ values for each individual was deemed its 'decision space' regarding when to initiate migration and how high to fly to receive maximum wind assistance at departure. We then similarly calculated cumulative AGR values (AGR_{cum}) that birds would have attained along their entire tracks at six geopotential heights had they departed on each of the 7 days preceding or following their actual departure date to determine how departure decisions corresponded with full flight performance. For the en route phase of each individual's flight, we calculated AGR_{10° values along the track at the six geopotential heights across distances spanning 10° of latitude for the north-south flights to and from New Zealand and across distances spanning 10° of longitude for the largely east-west flight from the Yellow Sea to Alaska. This 'option space' delineated choices that each individual could have made regarding how high to fly along its migratory track to attain maximum wind assistance. To generalize the extent to which a bird could optimize its wind profit by varying altitude, we calculated optimized AGR_{opt} values for each entire migratory track along which the bird was allowed to change altitude every 6 h to avail of the best wind conditions.

We constructed a series of linear mixed-effects models (LMM) to compare the potential consequences of different choices for when to depart on migration (decision space) and at what altitude to fly (option space). To test potential consequences of departure decisions on initial and overall performance for each flight leg, we modelled $AGR_{30\text{ h}}$ (during the first 30 h of a flight) and AGR_{cum} (along the entire flight), respectively, as a function of fixed effects for altitude (geopotential height), day relative to actual departure date (± 7 days), and their interaction; we included bird identification (ID) as a random effect. To evaluate the importance of altitudinal decisions while migrating through major latitudinal or longitudinal wind zones, we modelled AGR_{10° by fixed effects of 10° block, altitude, and their interaction, with bird ID included as a random effect. To assess potential consequences of altitudinal decisions on overall performance, we modelled AGR_{cum} along each entire flight track as a function of altitude (optimized and six fixed altitudes), with bird ID included as a random effect. Finally, to assess the overall potential efficiency of changing altitude during migration, we calculated for each individual the ratio of AGR_{opt} to the AGR_{cum} for each bird's best fixed-altitude across the entire migration leg. We used the Kruskal-Wallis test to determine whether efficiency differed between the three migration legs. For all mixed models we analysed ranked instead of raw AGR values because of small sample sizes and unequal error variances and used the Scheffé test (95% confidence) for multiple comparisons (Neter, Wasserman, & Kutner, 1990). For both the 'decision space' and 'option space' for each migratory flight we also constructed interpolated heat maps to illustrate the median AGRs that birds would have attained across time and space in the three-dimensional air

column. Statistical analyses were conducted using SAS software (SAS Institute, Inc., Version 9.2, Cary, NC, U.S.A.).

RESULTS

Over 4 study years (2006–2010), we tracked migrations of 24 godwits on one or more of the three migration legs for a total of 37 tracks (one leg: $N = 15$ birds; two legs: $N = 5$ birds; three legs: $N = 4$ birds; Fig. 1, Table 1). We tracked 18 birds northwestward from New Zealand to the major staging area in the Yellow Sea from 14 March to 10 April, 8 birds northeastward from the Yellow Sea to breeding grounds in Alaska from 1 May to 13 June, and 10 birds southward in autumn from Alaska back to New Zealand from 30 August to 17 October. The 37 tracks comprised 751 satellite-derived locations, including 327 (mean \pm SD = 18.2 ± 5.2 per bird), 124 (13.8 ± 6.1) and 300 (30.0 ± 14.5) locations for birds migrating from New Zealand to the Yellow Sea, from the Yellow Sea to Alaska and from Alaska to New Zealand, respectively. Godwits encountered markedly different wind scenarios at departure and en route during the three legs of their annual migration. These differed in intensity and duration, and across altitudes over scales ranging from local at departure sites to hemispheric across broad expanses of the central and western Pacific Ocean.

Winds Selected at Departure

New Zealand to the Yellow Sea

The northward migration between nonbreeding grounds in New Zealand and the major staging areas in the Yellow Sea was very direct, entailing a great-circle flight of about 10 000 km (Fig. 1). Birds departed New Zealand ($N = 18$) on 13 different days between mid-March and early April (Table 1). A comparison of $AGR_{30\text{ h}}$ (during the first 30 h of flight) that would have been attained if birds had flown their same routes but departed ± 7 days of actual departure dates (day = 0) showed significant effects of day (LMM: $F_{14,1513} = 39.50$, $P < 0.0001$) and altitude ($F_{5,1513} = 114.36$, $P < 0.0001$) but no interaction ($F_{70,1513} = 0.56$, $P = 0.999$). During the 15-day window (Fig. 2a, left panel), $AGR_{30\text{ h}}$ on day of departure was significantly better (lower) than the $AGR_{30\text{ h}}$ that would have been attained had birds departed 2–7 days earlier (Scheffé test: all $P < 0.0003$) but did not differ from the $AGR_{30\text{ h}}$ that would have been attained had they left 1–5 days later (Scheffé test: all $P > 0.16$). During the 15-day window, the best and least variable $AGR_{30\text{ h}}$ would have been attained by birds flying near the surface compared to any other fixed altitudes (Scheffé test: all $P < 0.04$; Fig. 2a, middle panel). To illustrate the decision and option spaces available for birds on this migration leg, we constructed an interpolated heat map of the median AGRs that would have been attained if birds had departed at various altitudes during the ± 7 days around the actual departure dates. Birds would have received the greatest wind assistance throughout the air column on the

actual departure dates and up to 4 days after departure (Fig. 2a, right panel).

A comparison of AGR_{cum} (along the entire flight track) that would have been attained if birds had flown their same routes but departed ± 7 days of actual departure dates showed similar results (not shown) to those for the initial $AGR_{30\text{ h}}$, with significant effects of day (LMM: $F_{14,1513} = 15.28$, $P < 0.0001$) and altitude ($F_{5,1513} = 449.58$, $P < 0.0001$) but no interaction ($F_{70,1513} = 1.11$, $P = 0.25$). The best (lowest) AGR_{cum} would have accrued to birds selecting their actual departure dates, although this did not differ significantly from the AGR_{cum} that birds would have attained if they had left any time during the 4 days preceding or following their actual departure dates (Scheffé test: all $P > 0.49$).

Yellow Sea to Alaska

After reaching the Yellow Sea, godwits refuelled on intertidal habitats for 5–7 weeks before they departed for their breeding grounds in Alaska in May. Nine marked birds departed the Yellow Sea on 8 different days between early May and early June (Table 1). A comparison of $AGR_{30\text{ h}}$ (during the first 30 h of flight) that would have been attained if birds had departed ± 7 days of actual departure dates showed significant effects of day (LMM: $F_{14,712} = 13.40$, $P < 0.0001$) and altitude ($F_{5,712} = 12.15$, $P < 0.0001$) but no interaction ($F_{70,712} = 0.90$, $P = 0.71$). During the 15-day window (Fig. 2b, left panel), the $AGR_{30\text{ h}}$ on the day of departure was significantly lower than the $AGR_{30\text{ h}}$ that would have been attained had birds departed during the previous 2 days or 6–7 days later (Scheffé test: all $P < 0.003$) but did not differ from the $AGR_{30\text{ h}}$ that would have been attained had they left 1–5 days later or 3–7 days earlier (Scheffé test: all $P > 0.73$). During the 15-day window, the $AGR_{30\text{ h}}$ for birds flying near the surface would have been significantly worse (higher) than those at any other fixed altitudes (Scheffé test: all $P < 0.0003$) except that immediately above at 800 m ($P = 0.09$; Fig. 2b, middle panel). Departures were characterized by a 24–36 h window during which median AGRs were most favourable (i.e. wind assistance was strongest) and most uniform throughout the entire air column (Fig. 2b, right panel).

A comparison of AGR_{cum} (along the entire flight track) that would have been attained if birds had flown their same routes but departed ± 7 days of actual departure dates showed similar results (not shown) to those for the initial $AGR_{30\text{ h}}$, with significant effects of day (LMM: $F_{14,712} = 10.74$, $P < 0.0001$) and altitude ($F_{5,712} = 2.73$, $P < 0.0001$) but no interaction ($F_{70,712} = 0.27$, $P = 1.00$). The best (lowest) AGR_{cum} would have again accrued to birds selecting their actual departure dates; this was significantly lower than the AGR_{cum} that birds would have attained had they left any time during the previous 3 days (Scheffé test: all $P < 0.05$) but similar to the AGR_{cum} had they left during the subsequent 5 days (Scheffé test: all $P > 0.91$).

Alaska to New Zealand and Eastern Australia

Autumn migration from Alaska to Australasia entailed the longest of the three nonstop flights, involving largely direct southward flights across the central Pacific (Fig. 1). Ten birds were tracked during departure on 10 different days between late August and early October (Table 1). A comparison of the $AGR_{30\text{ h}}$ (during the first 30 h of flight) that would have been attained if birds had departed ± 7 days of actual departure dates showed significant effects of day (LMM: $F_{14,801} = 11.93$, $P < 0.0001$) and altitude ($F_{5,801} = 12.01$, $P < 0.0001$) but no interaction ($F_{70,801} = 0.17$, $P = 1.00$). During the 15-day window (Fig. 2c, left panel), the $AGR_{30\text{ h}}$ on the day of departure was significantly lower than the $AGR_{30\text{ h}}$ that would have been attained had birds departed 2–6 days earlier (Scheffé test: all $P < 0.003$) but did not differ from the $AGR_{30\text{ h}}$ that would have been attained had they left the previous

Table 1
Departure chronology of satellite-tagged bar-tailed godwits

Migration leg	Year	Number of birds	Number of unique departure days	Departure period of tagged birds
New Zealand to Yellow Sea	2007	13	8	16 Mar–2 Apr
	2008	5	5	14–24 Mar
Yellow Sea to Alaska	2007	7	6	1 May–8 Jun*
	2008	2	2	5–13 May
Alaska to New Zealand	2006	5	5	30 Aug–23 Sep
	2007	4	4	30 Aug–7 Oct
	2010	1	1	25 Sep

* 8 June departure treated as an outlier by Battley et al. (2012); other departures in 2007 spanned 1–24 May.

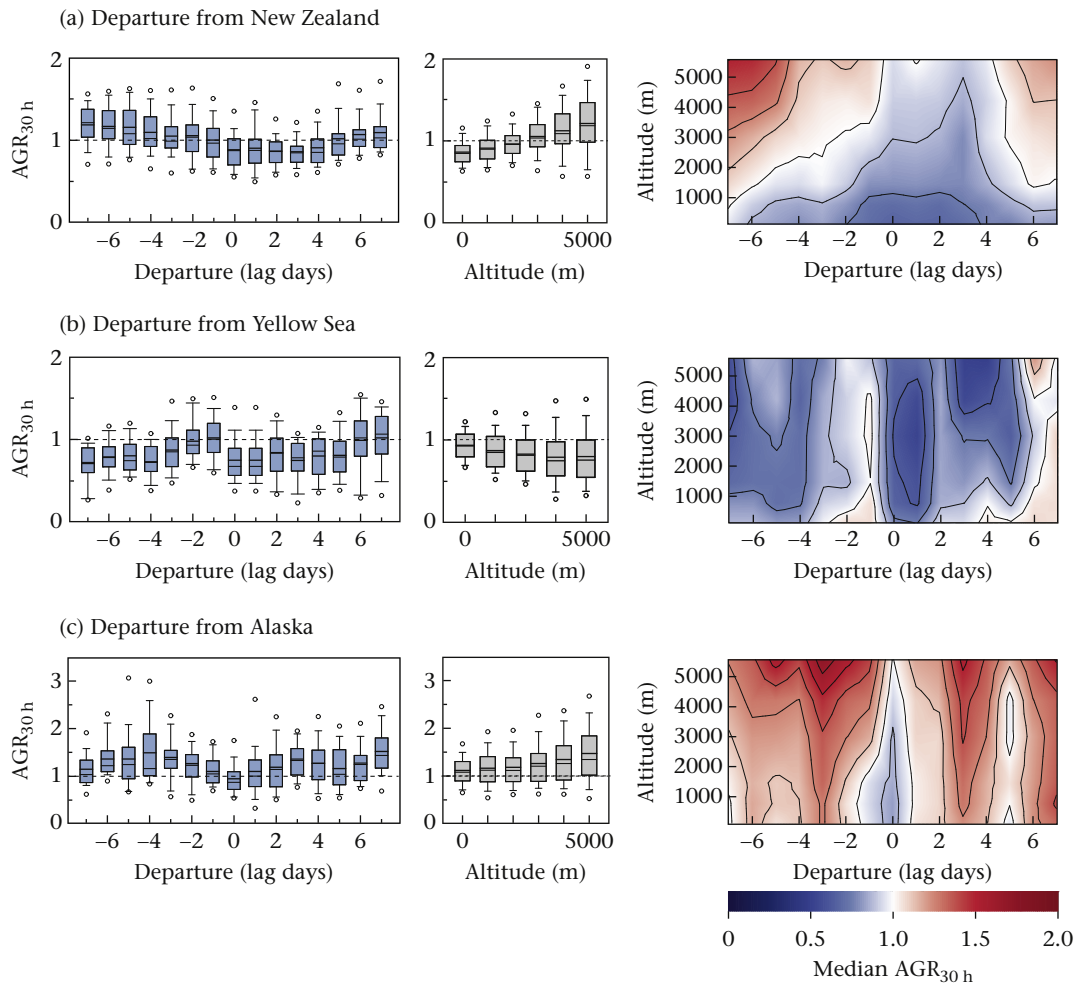


Figure 2. Box plots and interpolated heat maps of air-to-ground ratios (AGR_{30h}) that bar-tailed godwits would have accrued during the first 30 h of flight along their migration paths as a function of day relative to actual date of departure (day = 0) and altitude (m) for three migration legs. In box plots, thin horizontal line indicates median, thick horizontal line indicates mean, boundaries of the box include 25–75%, whiskers span 10–90%, and open circles denote outliers. Values for departure days are averaged across six potential altitudes; values for altitude are averaged across 15-day potential departure windows. In heat maps, blue shading denotes wind conditions assisting flight ($AGR < 1$); red shading denotes wind conditions impeding flight ($AGR > 1$) for median AGR s that would have been attained if birds had departed at various altitudes during the ± 7 days around actual departure dates. Lines denote contour intervals of 0.125 AGR . Rows illustrate conditions during departure from (a) New Zealand to the Yellow Sea ($N = 18$), (b) the Yellow Sea to Alaska ($N = 9$) and (c) Alaska to New Zealand or eastern Australia ($N = 10$).

day or 1–2 days later (Scheffé test: all $P > 0.23$). During the 15-day window, the best and least variable AGR_{30h} would have been attained by birds flying near the surface, but this differed significantly only from those at the two highest of the fixed altitudes (> 4000 m; Scheffé test: both $P < 0.002$; Fig. 2c, middle panel). Departure conditions on this leg differed markedly from those of the two other legs. Departures from Alaska were characterized by a relatively narrow 48 h window during which median AGR s were favourable (i.e. with weak to moderate wind assistance) from the surface to about 4000 m (Fig. 2c, right panel). Such conditions were bounded on either side by periods of strong wind resistance, including long pulses of 12 h to 48 h that increased in strength with altitude.

A comparison of the AGR_{cum} (along the entire flight track) that would have been attained if birds had flown their same routes but departed ± 7 days of actual departure dates showed similar results (not shown) to those for the initial AGR_{30h} , with significant effects of day (LMM: $F_{14,801} = 11.63$, $P < 0.0001$) and altitude ($F_{5,801} = 27.87$, $P < 0.0001$) but no interaction ($F_{70,801} = 0.30$, $P = 1.00$). Again, the best (lowest) AGR_{cum} would have accrued to birds selecting their actual departure dates, although this did not differ significantly from

the AGR_{cum} that birds would have attained had they left any time during the 2 days preceding or 5 days following their actual departure dates (Scheffé test: all $P > 0.19$).

Winds Selected En Route

New Zealand to Yellow Sea

AGR_{10° of godwits during their migration from New Zealand to the Yellow Sea varied significantly both by 10° latitudinal segment (LMM: $F_{7,673} = 65.44$, $P < 0.0001$) and altitude ($F_{5,673} = 9.76$, $P < 0.0001$), and the effect of altitude varied by segment ($F_{35,673} = 6.80$, $P < 0.0001$). During the initial part of the flight, wind conditions were favourable ($AGR_{10^\circ} < 1$) throughout most of the air column but optimal near the surface (Fig. 3a, left panel). Near the equator, conditions changed and optimal AGR_{10° with tailwind assistance would have been attained by birds flying at higher altitudes. Altitudinal conditions changed again during the final portion of the flight as birds approached the Yellow Sea, where they would have encountered very strong wind resistance at the highest altitudes and the most favourable conditions (mostly weak resistance) near the surface.

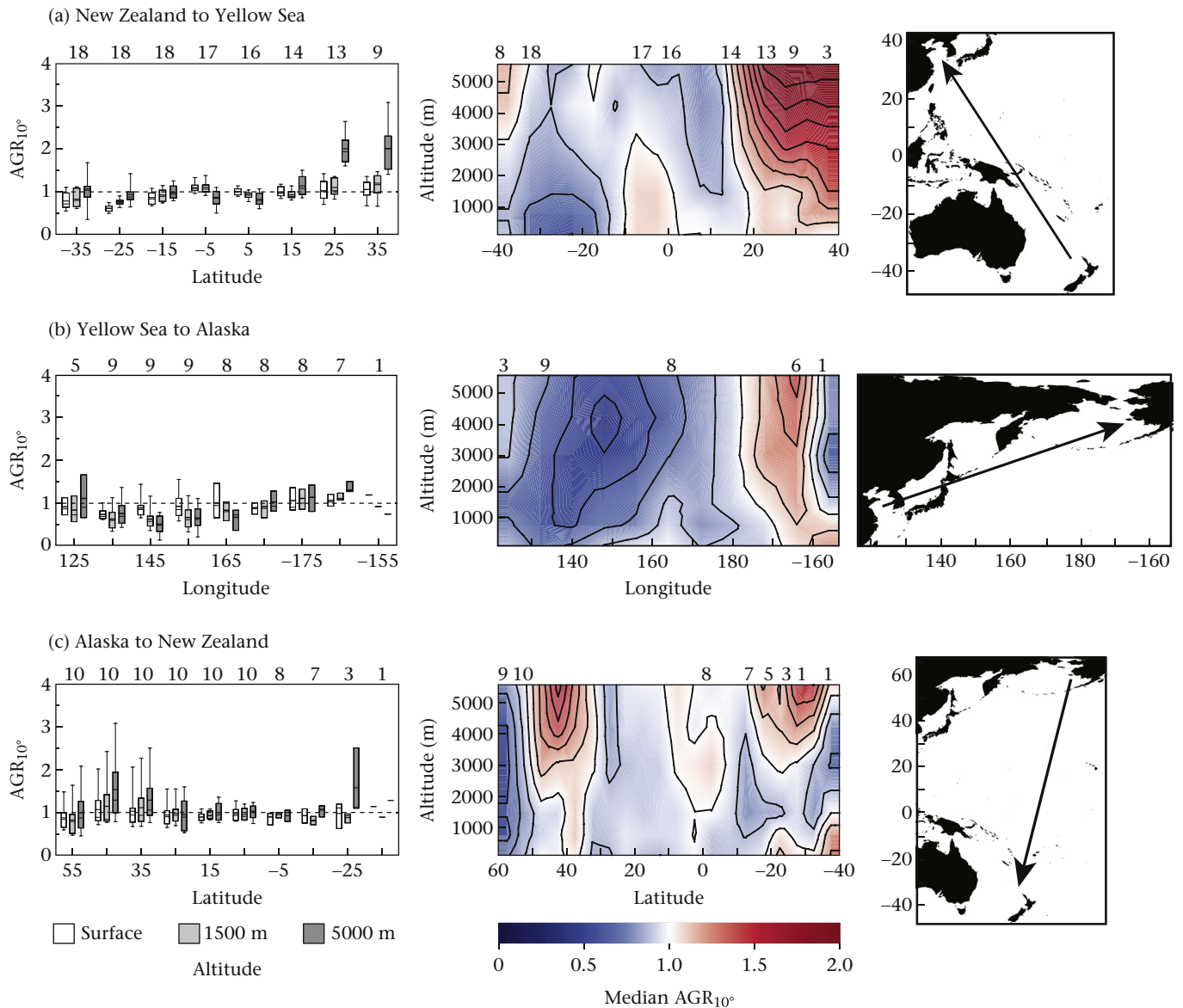


Figure 3. Box plots and interpolated heat maps of air-to-ground ratios (AGR_{10°) of bar-tailed godwits as a function of altitude (m) and 10° blocks of latitude (or longitude) en route during three migration legs. In box plots, thin horizontal line indicates median, thick horizontal line indicates mean, boundaries of the box include 25–75%, and whiskers span 10–90%. In heat maps, blue shading denotes wind conditions assisting flight ($AGR < 1$); red shading denotes wind conditions impeding flight ($AGR > 1$) for median AGR s that birds would have attained by flying at different altitudes along their routes. Lines denote contour intervals of 0.125 AGR . Rows illustrate conditions en route from (a) New Zealand to the Yellow Sea, (b) the Yellow Sea to Alaska and (c) Alaska to New Zealand or eastern Australia, as shown in the maps to the right. Sample sizes (shown along the top edge of each panel) diminish with distance as birds landed short of their final destinations, or data reception stopped during flight.

Yellow Sea to Alaska

Unlike the mostly direct flight path taken by birds between New Zealand and the Yellow Sea, routes taken by godwits en route to Alaska deviated considerably from a great-circle track, some arching northward and others southward for much of their flight (Fig. 1). During these flights, AGR_{10° varied significantly both by 10° longitudinal segment (LMM: $F_{8,322} = 26.53$, $P < 0.0001$) and altitude ($F_{5,322} = 4.78$, $P < 0.0001$), but the effect of altitude did not vary significantly by segment ($F_{40,322} = 1.06$, $P = 0.38$). From the principal departure site in the eastern Yellow Sea ($\sim 125^\circ$ E) to about the Eastern Aleutian Islands ($\sim 175^\circ$ E), a distance of about 4500 km, most godwits, no matter their position in the air column, would have received significant wind assistance (Fig. 3b, left panel). One exception, godwit E8, embarked on a flight path at about 160° E longitude that resulted in an abrupt transition into persistent

headwinds that ultimately caused the bird to abort its migration and return eastward (with tailwinds) to the coast of Russia (Fig. 4b, Supplementary Fig. S1). Compared to birds on the flight to the Yellow Sea, individuals en route to Alaska experienced much more variable conditions as evidenced by larger interquartile ranges (Fig. 5). Past 175° W, conditions changed from wind assistance to resistance that was weak below 1000 m but increased in strength at higher altitudes (Fig. 3b, middle panel).

Alaska to New Zealand and Eastern Australia

The southward migration of most satellite-tracked birds included a slight initial easterly deviation from what would mostly be a great-circle track (Fig. 1). During these flights, AGR_{10° varied significantly both by 10° latitudinal segment (LMM: $F_{9,405} = 4.13$, $P < 0.0001$) and altitude ($F_{5,405} = 3.33$, $P = 0.006$), but the effect of altitude did not

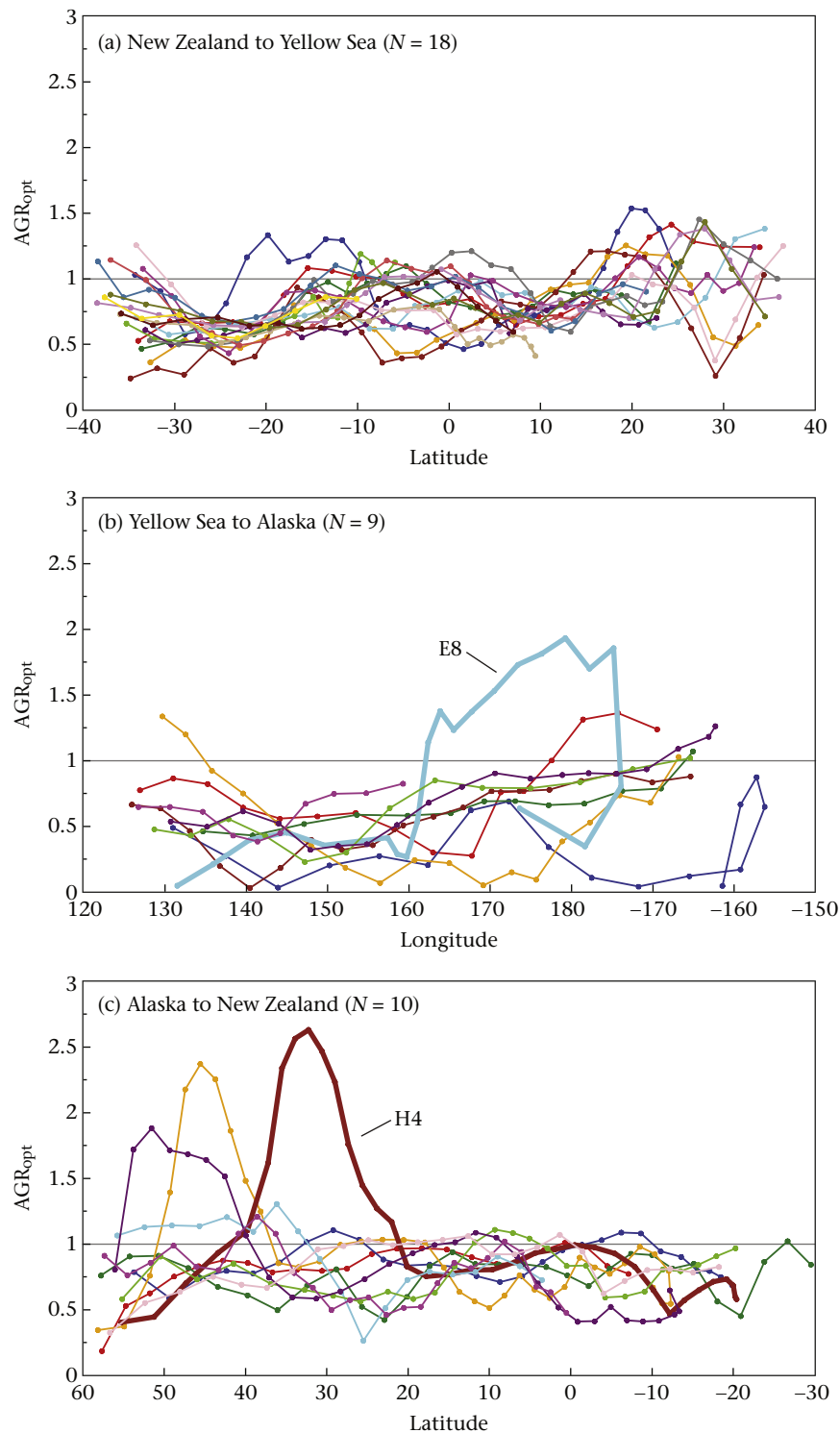


Figure 4. Optimized air-to-ground ratios (AGRs) for individual bar-tailed godwits across a latitudinal (or longitudinal) gradient for each migration leg. The ratio was optimized by allowing flight altitude to change every 6 h (if necessary) to utilize the most favourable wind conditions along each bird's track. Although such flight behaviour is purely speculative, the results provide a theoretical 'best case' scenario. Among all tracked birds, godwits E8 (bold blue line) and H4 (bold red line) encountered some of the most adverse wind conditions during migration (see [Supplementary Figs S1, S2](#)).

vary significantly across the flight ($F_{45,405} = 0.44$, $P = 0.999$). The most favourable wind conditions occurred at lower altitudes throughout the flight (Fig. 3c, left panel). During the first 1000 km of the flight, almost all godwits would have received wind assistance by flying low (Fig. 3c, left panel). During transit through the zone of

Westerlies in the North Pacific from approximately 55° N to 30° N, godwits encountered highly variable atmospheric conditions (Fig. 3c, left panel), with 3 of 10 birds encountering severe wind resistance even at optimal altitudes (AGR_{opt} 1.9–2.6; Fig. 4c). In a particularly extreme case, godwit H4 encountered a rapidly developing cyclone in

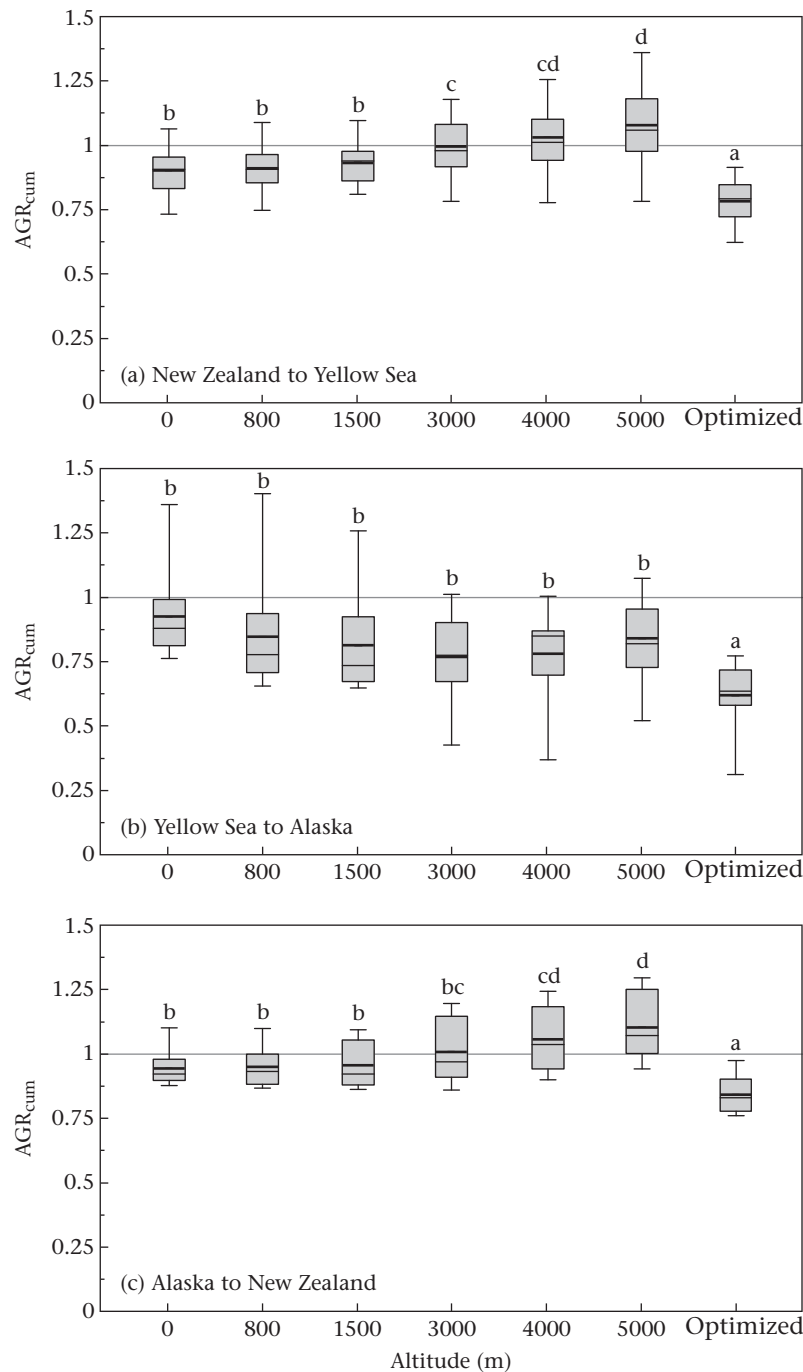


Figure 5. Box plots of cumulative air-to-ground ratios (AGR_{cum}) modelled across the entire flight for bar-tailed godwits flying at one of six fixed altitudes compared with an optimized value, in which godwits were modelled to change altitude along their tracks every 6 h to optimize wind assistance. In box plots, thin horizontal line indicates median, thick horizontal line indicates mean, boundaries of the box include 25–75%, and whiskers span 10–90%. Different letters above box plots indicate significantly different AGR_{cum} for different altitudinal options ($P < 0.05$). $AGR < 1$ indicates net wind assistance during the flight; $AGR > 1$ indicates net wind resistance. Panels illustrate conditions during migratory legs from (a) New Zealand to the Yellow Sea ($N = 18$), (b) the Yellow Sea to Alaska ($N = 9$) and (c) Alaska to New Zealand or eastern Australia ($N = 10$).

the North Pacific ($\sim 35^\circ\text{N}$, 158°W) and had to struggle through an uncharacteristically long fetch of headwinds directly in its flight path (Supplementary Fig. S2). Between 30°N and 20°S , a distance of almost 5500 km, conditions for most birds remained favourable, especially below 2000 m altitude. The single bird tracked all the way to New Zealand encountered slight surface headwinds near its destination (Fig. 3c). The least favourable and most variable wind conditions along the flight tracks occurred at high altitudes near 45°N and 25°S (Fig. 3c, left panel).

Optimal Flight Altitude

For each of the three flights (Fig. 5), AGR_{cum} , a measure of flight efficiency across the entire migratory flight, was significantly dependent upon the altitude at which godwits selected to fly (LMM: New Zealand to the Yellow Sea: $F_{6,102} = 78.16$, $P < 0.0001$; the Yellow Sea to Alaska: $F_{6,48} = 10.57$, $P < 0.0001$; Alaska to New Zealand: $F_{6,54} = 54.25$, $P < 0.0001$). For all three flights, godwits would have achieved significantly better AGR_{cum} by varying

altitude along their routes to optimize wind conditions rather than by flying consistently at any of the six fixed altitudes between 100 m and 5000 m that we investigated (Scheffé test: all $P < 0.03$). For the flights to and from New Zealand, the best fixed altitudes at which to fly would have been at or below 1500 m; most individuals would have realized net wind resistance ($AGR_{cum} > 1.0$) at higher altitudes but AGR_{cum} would have been least variable at lower altitudes (Fig. 5a, c). In contrast, altitudinal wind conditions were highly variable along individual tracks from the Yellow Sea to Alaska, and no single fixed altitude was significantly better than the others (Fig. 5b). Most birds would have received net wind assistance ($AGR_{cum} < 1.0$) by flying steadily at altitudes above 3000 m, and fixed-altitude flights below that would have been highly unfavourable only to one bird, E8 (Fig. 5b).

If godwits had optimized wind conditions on the three flight legs by switching altitude when advantageous, all individuals would have realized net wind assistance (median $AGR_{opt} = 0.63–0.83$; Fig. 5). Such switches would have reduced AGR_{cum} by $12 \pm 5\%$ compared to those achieved by flying at the single-best fixed altitude throughout their flights, with similar efficiencies attained on the three legs (Kruskal–Wallis test: $\chi^2_2 = 2.71$, $P = 0.26$). To achieve such optimization, birds would have averaged 5 ± 2 upward shifts in altitude (and compensating downward shifts) totalling an average of 10 900 m (± 3370 m) of upward elevation change over an average of 23.6 ± 6.76 h flight segments per individual. Most of the optimal upward shifts (56% of 192) would have involved altitudinal changes of less than 1500 m and only 15% would have exceeded 4000 m.

DISCUSSION

That birds are capable of directed flights lasting 1 week or more without stopping to refuel was speculative less than a decade ago (Gill et al., 2005; Gill et al., 2009; Hedenström, 2010). Our results from satellite tracking of individual godwits confirm that not only do birds make such migrations (Battley et al., 2012; Gill et al., 2009), but their ability to do so involves strategic decision and option spaces about when and where to fly within the highly dynamic wind regimes they traverse. We have shown that godwits' selectivity of wind conditions at departure, even when not critical, generally assures the 'best' decision for flight efficiency during the initial segment of the long, nonstop flight. More importantly, the departure decision generally ensures the best conditions for the entire, multiple-day flight. For optimal migration theory, our findings underscore the fundamental importance of understanding the behavioural and ecological elements underpinning wind selectivity by migratory species, especially extreme endurance migrants (e.g. Åkesson & Hedenström, 2000; Alerstam, 1979, 2011; Alerstam & Hedenström, 1998; Alerstam & Lindström, 1990; Grönroos et al., 2012; Liechti & Bruderer, 1998).

Wind Selectivity at Departure

For each of the three migration legs godwits exhibited wind selectivity at departure. For birds leaving New Zealand on northward migration, winds during the departure period were generally benign and selectivity was not critical, yet birds still chose the best day (most favourable AGR), or the start of a series of good days, on which to depart. Our findings corroborate those of Conklin and Battley (2011), who found that unfavourable departure conditions occurred infrequently for godwits leaving New Zealand, but that some birds did alter individual migration schedules to maximize initial wind assistance. For birds continuing northeast from the Yellow Sea, selectivity was more important, especially since the Yellow and Japan seas comprise a region of cyclogenesis (Adachi &

Kimura, 2007; Mesquita et al., 2010; Whittaker & Horn, 1984) with storms that bring elements of variability and unpredictability into the decision space. All but one bird selected departure dates providing an option of significant wind assistance (Fig. 4) and they attained this by departing on the first day following a marked change in winds that produced favourable AGRs. The periodicity of AGRs ± 7 days of actual departure dates reflects regional wind patterns associated with the local formation and passage of weather systems, usually cyclones.

Wind selectivity was similarly paramount for godwits departing Alaska (Gill et al., 2005; Gill et al., 2009) where, like the Yellow Sea, the juxtaposition of departure sites and storm tracks enables finely attuned departure decisions. Whereas in the Yellow Sea 4- to 6-day periods of favourable conditions were interrupted by 1–2 days of adverse conditions, birds departing Alaska faced a more sinuous array of conditions that worsened and then improved over more compressed 2- to 4-day periods. Nevertheless, 9 of the 10 birds either selected the optimal departure date within the surrounding 2-week period or left within 1–2 days of the optimal date and at the start of a narrow window of stable or improving wind conditions. The 10th individual left the day after the optimum departure date but in the face of 1 week of worsening conditions.

The seasonal occurrence, frequency and strength of cyclones in regions where godwits depart appear to drive the degree of their wind selectivity. For example, over the Tasman Sea near New Zealand there is both a marked decrease by February and early March in the frequency of cyclones and a northward shift in the South Pacific Anticyclone belt (Lim & Simmonds, 2002) that builds high pressure. These seasonal shifts combine to create prolonged favourable conditions and thus low selectivity. In contrast are the two North Pacific departure sites, the Yellow Sea and southwestern Alaska. Both are affected by cyclones during departure periods and selection of synoptic-scale winds is strategic for optimal departure. Cyclones originating in the Yellow Sea region decline in frequency during spring but still occur during May (Xu, Xu, Xie, & Wang, 2011), producing markedly variable wind conditions as they track eastward across the North Pacific (Adachi & Kimura, 2007; Mesquita et al., 2010; Whittaker & Horn, 1984). When birds depart Alaska during September through October, the Aleutian Low is deepening and the frequency and strength of cyclones are approaching annual highs (Mesquita et al., 2010). Our results suggest that birds have evolved a sensory mechanism to assess departure conditions as storms repeatedly form and pass through these regions. At departure sites, godwits are likely well situated to predict the position, proximity and quality of developing or transiting cyclones. We believe the most likely cue signalling a departure window at such sites is a change in barometric pressure and an associated change in wind direction as cyclones form near or pass by departure sites. There is mounting evidence that baroreception is highly refined in most birds (Metcalf, Schmidt, Kerr, Guglielmo, & MacDougall-Shackleton, 2013; O'Neill, 2012).

Wind Selectivity En Route

Once birds depart an area, they can choose where to fly laterally and vertically in the air column to maximize wind profitability and hence minimize the cost of transport (Alerstam, Hedenström, & Åkesson, 2003; Alerstam & Lindström, 1990). Our tracking data revealed two segments of the flights where birds deviated from otherwise mostly great-circle routes (Battley et al., 2012), both associated with the North Pacific storm track. The first involved most of the birds en route from the Yellow Sea to Alaska and entailed flights that occurred mostly far south ($21–41^\circ$ of latitude) of a direct route. Indeed, towards the end of their flight several godwits had to make abrupt northward, open-ocean course

changes of 20–50° to reach initial landfall in southwest Alaska. This selected flight corridor coincides with principal storm tracks in the North Pacific (Adachi & Kimura, 2007; Anderson & Gyakum, 1989; Mesquita et al., 2010; Whittaker & Horn, 1984) whereby birds would receive significant wind assistance throughout most of the flight by flying in association with the southern periphery of rapidly moving west-to-east cyclones (e.g. Hameed, Norwood, Flanagan, Feldstein, & Yang, 2009). Spring cyclones in the North Pacific track at about 12–15 m/s (Mesquita et al., 2010), or roughly the average track speed (14.8 ± 1.7 m/s) recorded for godwits along the entire flight between the Yellow Sea and Alaska (Battley et al., 2012). At both the principal (Sea of Japan) and secondary (south of the Aleutian Islands) loci of cyclogenesis along the migration corridor, where systems often deepen and wind speeds increase, we found the track speed of birds increased by about 25% to 19.6 ± 4.3 m/s (range 12.2–32.8; $N = 34$ records from 8 birds; Gill, n.d.). Implicit in the increased track speeds is a strategy to select locations where winds minimize energy expenditure and maximize range (energy-selected migrant). We presume such decisions are made in part to ensure that birds arrive on the breeding grounds on time and with sufficient stores to initiate the reproductive phase of the annual cycle (Drent, 2006; Vézina, Williams, Piersma, & Morrison, 2012).

The second example of lateral deviation along a flight corridor involved birds shortly after departing Alaska on a trajectory for New Zealand. Flying southward across the North Pacific required them to cross the zone of Westerlies (~50–30° N) where they sometimes encountered predictable, significant wind resistance ($AGR_{opt} = 1.9$ –2.6). Faced with prevailing southwest winds, godwits chose to drift east of a direct route (see Green, Alerstam, Gudmundsson, Hedenström, & Piersma, 2004) and then when they were farther south and into the southeast-flowing Trade Winds, they reoriented towards New Zealand and compensated their earlier drift under conditions of wind assistance. Thus, this regular course deviation reflects consistent behavioural choice in orientation to capitalize on wind drift through predictable alternating zones of winds.

An important but unexpected finding was that departure decisions enabled godwits to optimize wind selectivity over flights lasting many days. Favourable conditions at departure, however, did not always translate into predictable conditions en route, particularly for the two segments crossing the North Pacific, which are regions of rapid cyclogenesis. For example, godwit E8 departed the Yellow Sea under very favourable conditions (Fig. 4b) but was overtaken by a cyclone that rapidly deepened when it merged with a resurging extratropical typhoon. E8 became entrained in the northern edge of this system as it crossed into the Bering Sea (Supplementary Fig. S1). Although E8 eventually reached Alaska she did not breed, likely because after fighting prolonged headwinds she arrived on the breeding grounds having depleted not only the nutrient stores carried for arrival and reproduction but also the 'last resort' reserves (Lindström & Piersma, 1993). Godwit H4 departed Alaska also with favourable winds (Fig. 4c) but soon thereafter was caught between a rapidly developing cyclone and a massive ridge of high pressure, leaving no option but to fly directly into an uncharacteristically long fetch of strong headwinds (Supplementary Fig. S2). Such weather systems develop within hours, move quickly, and thus by nature are unpredictable and variable (Allen, Pezza, & Black, 2010; Chen, Kuo, Zhang, & Bai, 1992; Lim & Simmonds, 2002; Yoshida & Asuma, 2004). Although infrequent during migration periods (Chen et al., 1992), such conditions may engender severe fitness costs in terms of reduced reproduction or survival. Both of these examples illustrate, however, that 'favourable' AGRs may result when individuals that are facing insurmountable headwinds suddenly abandon the course to their

intended destination and instead drift with the prevailing winds to an alternate destination. In changing their flights, E8 and H4 showed the flexibility in reaction to wind that many authors (Shamoun-Baranes & van Gasteren, 2011 and citations therein) have proffered as necessary in order for individuals to take advantage of dynamic and heterogeneous atmospheric conditions.

Optimized Altitudes

Choices pertaining to departure decisions and where to fly laterally within the air column clearly influence energetic efficiency of extreme endurance migrants, but vertical placement in the air must also bear on this. We found that winds varied considerably with altitude, both among and along the three flight segments, and thus godwits were presented with a suite of decisions about where to fly vertically to maximize wind profitability. Other studies that have addressed flight altitude have found that wind profitability can be greatly increased by flying at different altitudes at different times of day (e.g. Alerstam & Gudmundsson, 1999; Bruderer, Underhill, & Liechti, 1995; Conklin & Battley, 2011; Gauthreaux, 1991; Green, 2004; Gudmundsson, Alerstam, Green, & Hedenström, 2002; Klaassen & Biebach, 2000; Newton, 2008 and citations therein; Piersma et al., 1990; Schaub, Liechti, & Jenni, 2004). Although we did not directly measure flight altitude in our study, we have no reason to believe that godwits are not selecting the best altitude to minimize their cost of transport (Piersma, 2011a; Weber, 2009), optimize osmotic homeostasis (Gerson & Guglielmo, 2011; Klaassen, 2004; Landys, Piersma, Visser, Jukema, & Wijker, 2000), or both (cf. Kemp et al., 2013). For example, our modelling exercise indicated that it was better to fly low (<1500 m) than high except when crossing the equator during flights between New Zealand and the Yellow Sea (Fig. 3c). Throughout most of the flight between the Yellow Sea and Alaska, birds would have received wind assistance throughout the air column, but the best AGRs would have come from flying high, between 1500 and 5000 m, until approaching Alaska. The greatly increased track speeds we recorded on this segment suggest that birds were indeed at high altitudes, possibly even within the lower bounds of the North Pacific low-level jet stream in this region that often descends below 700 hPa (3000 m) height (Liechti & Schaller, 1999; Yoshida & Asuma, 2004). Studies of other species have shown that migrants can vary their altitude to maximize wind assistance (Dokter et al., 2011; Dokter et al., 2013; Gauthreaux, 1991; Liechti, 2006; Shamoun-Baranes et al., 2006), and recently a black-tailed godwit, *Limosa limosa*, in Europe was tracked as it ascended within 2.5 h from near sea level to a zone of much more favourable winds at greater than 4500 m altitude (Bouten, Senner, & Piersma, n.d.). Thus we predict that such behavioural choices will also be confirmed for bar-tailed godwits once new GPS technology is deployed to track their altitudinal movement on flights over the vast Pacific Ocean.

Longer-term Predictability and Variability

Bar-tailed godwits are relatively long-lived birds with increasing evidence of an average life span approaching 10 years (mean \pm SD age at recapture = 7.5 ± 3.7 years, range 2.6–17.2 years, $N = 77$; Riegen, n.d.). As such, individuals have had to integrate into their migration strategies not only seasonal aspects of climate but also low-frequency fluctuations between the ocean and atmosphere that occur throughout the Pacific on annual to decadal timescales (e.g. ENSO, PDO). These fluctuations include teleconnected perturbations resulting from ENSO and PDO that extend throughout mid-latitudes of the North and South Pacific and include shifts in the strength and position of the Aleutian Low, the ITCZ, the South

Pacific Convergence Zone and the Trade Wind belts. These in turn result in anomalies in wind fields and the genesis, intensity and tracks of storms that, over existing migration corridors, can create both favourable and unfavourable conditions (Chand & Walsh, 2011; Froude, 2009; Larkin & Harrison, 2002; Mantua & Hare, 2002; Mesquita et al., 2010; Overland et al., 1999; Whysall, Cooper, & Bigg, 1987). Although beyond the scope of this study, we predict that additional analyses will demonstrate that godwits have ample and flexible enough response behaviours to adapt to such longer-term changes (cf. Conklin, Battley, & Potter, 2013; Piersma, 2011b). The question is whether their behavioural responses will be able to match future rates of meteorological change, which are as yet highly uncertain but generally projected to be extreme under climate-change scenarios (e.g. Bengtsson, Hodges, & Roeckner, 2006; Emanuel, Sundararajan, & Williams, 2008; Oouchi et al., 2006; Vavrus, Holland, Jahn, Bailey, & Blazey, 2012).

Conclusions

We have shown that Pacific wind regimes present bar-tailed godwits with numerous decisions related to when (decision space) and where (option space) to fly during each of the three legs of their annual migration. We have presented evidence that birds are able to assess both the predictability and variability of atmospheric conditions, particularly wind. Indeed, the days on which godwits departed the three staging sites conferred the greatest overall wind assistance not only immediately after departure but also throughout their long-distance flights, suggesting a level of behavioural cognition related to atmospheric teleconnections that was heretofore unknown among migratory birds. But our study also suggests that godwits have limits to their ability to sense and respond to rapidly developing stochastic events during the en route phase of their migrations. Lastly, our results provide new insights into the highly adaptive orientation performance of extreme endurance migratory birds (see, e.g. Klaassen, Hake, Strandberg, & Alerstam, 2011), which likely involves some form of position-fixing mechanism (Luschi, 2013) that may allow birds to avail of winds and compensate for wind drift (sensu Chapman et al., 2011; McLaren, Shamoun-Baranes, & Bouten, 2012). It is still unknown what mechanisms godwits use for orientation, but it has recently been shown that the geomagnetic bicoordinate map used elsewhere is not present over most of the Pacific Basin (Boström, Åkesson, & Alerstam, 2012; but see Luschi, 2013). Worthy of further assessment is the idea that prevailing winds and ocean waves may create cues in the form of an infrasonic map (Hagstrum, 2013).

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Supplementary Material

Supplementary material for this article is available in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.01.020>.

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Appendix

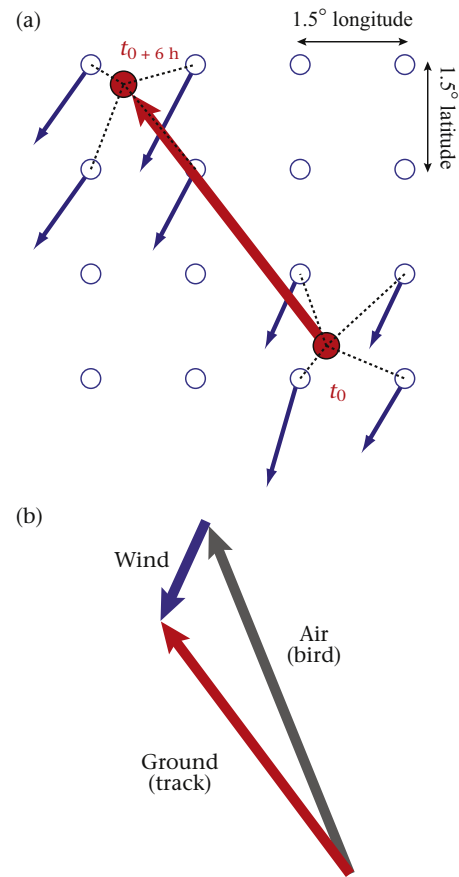


Figure A1. Method for decomposing tracking vectors of bar-tailed godwits. (a) Starting and ending locations for each 6 h tracking vector (red) were spatiotemporally co-registered with wind data from the ERA-Interim global reanalysis. Winds at the two tracking end points were each calculated as an inverse-distance weighted average of winds (blue arrows) at the four surrounding reanalysis grid points (circles). (b) An average 6 h wind vector (based on the two end points) was subtracted from the ground (tracking) vector to derive the air vector.